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Comparing free-ranging and captive populations reveals intra-specific variation in aging rates in large herbivores

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ABSTRACT

Although evidence that survival decreases with age in animal species is compelling, the existence of variation in aging rates across different populations of a given species is still questioned. Here, we compared aging rates of 22 pairs of ruminant species living in captive and free-ranging conditions. Based on the recent suggestion that feeding niche is a key factor influencing aging in captivity, we also investigated whether a species' natural diet influences the aging rates of captive ruminants relative to their wild conspecifics. We found that aging rate in a given species was higher under free-ranging conditions than in captivity, which provides the first evidence of consistent aging rate variation within species. Additionally, our study clearly demonstrates that differences in aging rates between captive and free-ranging ruminants increased as species were more specialized on grass diets.

Keywords: Actuarial senescence; age-specific mortality; comparative demography; life-history traits; mammals; zoo

1. Introduction

Empirical evidence accumulated during the last two decades shows that mortality rate increases with age during adulthood in animal and human populations (Finch, 1990; Holmes and Austad, 1995; Gaillard et al., 2003; Nussey et al., 2013). Moreover, intensive long-term studies of wild populations have revealed that the intensity of this increase of mortality with age, called rate of aging or rate of actuarial senescence, markedly differs between sexes and among species (Loison et al., 1999; Gaillard et al., 2003, 2004; Clutton-Brock and Isvaran, 2007; Ricklefs, 2008, 2010a). However, the extent to which the aging rate is a species-specific constant for a given sex or varies within species according to environmental conditions is questioned (Ricklefs and Scheuerlein, 2001; Austad, 2011). For instance, in the fly *Telostylinus angusticollis*, males living in the wild have a higher aging rate than males living under laboratory conditions (Kawasaki et al., 2008), while for female baboons aging rate does not show variation between captive and wild populations (Bronikowski et al., 2002; see also Vaupel, 2010 for a discussion on the homogenous aging rates found across human populations). Therefore, the study of aging rate variation within species is a timely topic in evolutionary ecology of aging, especially in non-laboratory organisms (Nussey et al., 2013). Assessing the magnitude of intra-specific variation in aging rates could notably provide new insights on the importance of the gene by environment interaction in the aging process (Promislow et al., 2006) and to bio-gerontological studies focused on lifespan extensions (Partridge, 2010).

From a life history perspective, aging can be interpreted as a trade-off ('disposable-soma theory': Kirkwood, 1977) where any increase in reproductive effort during early life should ultimately lead to a higher rate of actuarial or reproductive aging (Kirkwood, 1977; Kirkwood and Austad, 2000). Thanks to the availability of longitudinal data from long-term monitoring of populations and to the recent development of statistical methods (e.g. Rebke et al., 2010), the relationships between reproductive effort during early life and decline in

various reproductive traits at later stages are now well documented (Descamps et al., 2008; Orell and Belda, 2002; Reed et al., 2008; Robinson et al., 2012). For instance, in female great tits (*Parus major*) rates of reproductive aging (on fledging and recruitment production) increase with early life reproductive effort and are higher for immigrant individuals that spent early ages in more hostile environments (Bouwhuis et al., 2010). Similarly, in feral horses (*Equus caballus*), survivorship and longevity were increased when immunological contraception was introduced as a management tool (Turner and Kirkpatrick, 2002; Kirkpatrick and Turner, 2007). However, evidence of variation in the rate of aging in response to early environmental conditions remains scarce and, to our knowledge, limited (at least in mammals) to red deer (*Cervus elaphus*), in which females born at high population density have higher aging rates in both survival and reproduction than females born at low density (Nussey et al., 2007). Therefore, although some intra-specific studies have successfully correlated variation in environmental conditions with variation in survival (e.g. Tatar et al., 1997; Duyck et al., 2010), evidence that environmental conditions can influence aging rate per se remains scarce.

A promising approach to study variation in aging rate is to compare populations living in two contrasted environments such as captive (or laboratory) versus free-ranging conditions (Mason, 2010). Moreover, such a comparison allows understanding proximate causes of increases in age-related mortality (Ricklefs, 2000; Ricklefs and Scheuerlein, 2001). If adult mortality is mainly determined by an increased susceptibility to environmental factors (e.g. predation, inclement weather, antagonistic contests for resources or mating opportunities) aging rate should be higher in wild than in captive populations (Ricklefs and Scheuerlein, 2001) because individuals in zoos receive veterinary care, are protected against predation and starvation, and may additionally be limited in their reproduction (Asa and Porton, 2005). On the contrary, between-population differences are not expected to occur when adult mortality is mainly caused by physiological deterioration of individuals when aging (e.g. heart or

autoimmune diseases, cancer) that are often considered to be genetically fixed (Ricklefs and Scheuerlein, 2001). Evidently, in the real world, both intrinsic and environmental factors will interact (Boyce et al., 2006). In a pioneering inter-specific comparison of captive and free-ranging populations, Ricklefs (2000) reported that birds from zoos and wild populations have similar aging rates, suggesting that environmental factors do not influence the increase of mortality rate with age in birds. However, due to their flying abilities, birds might circumvent predation or harsh environmental conditions more easily even when individuals become older (Holmes and Austad, 1994), which suggests that the variance in aging rate could be lower in flying than in terrestrial species.

Since longevity records are often held by zoos (Carey and Judge, 2000), it is generally considered that animals perform better in captivity than in free-ranging conditions. However, Mason (2010) recently emphasized that this predominant idea requires caution because survivorship can sometimes be lower in captive compared to free-ranging populations. To understand better what ecological factors might shape differences in aging rate or other measures of survival performance, comparative studies controlling for phylogeny on species living in these two contrasted environments are required (Mason, 2010). A first step in this direction was recently achieved by Müller et al., (2010), who reported a higher life expectancy for captive as compared to free-ranging reindeer (*Rangifer tarandus*), whereas wild roe deer (*Capreolus capreolus*) performed better than captive ones. These findings suggest that zoos might have more difficulties in maintaining browsers as compared to mixed-feeders or grazers, which is supported by the positive relationship reported between relative life expectancy and percentage of grass in the diet across 78 species of ruminants kept in captivity (Müller et al., 2011). In this study, we first tested for aging rate variation within species using captive populations and their free-living counterparts for 22 ruminant species. Ungulates are indeed an especially appropriate group for performing such analyses because of the availability of several long-term monitoring of populations, allowing reliable estimates of

age-specific mortality for several species (Nussey et al., 2008). Then, based on the suggestion that diet is a key factor influencing survivorship in captivity (Clauss et al., 2003), we investigated whether a species' natural diet influences the difference of aging rate between captive and wild populations of ruminants. Since performance in contrasted environments can also vary between sexes (e.g. red deer, Müller et al., 2010), we lastly tested for between-sex differences of aging rates in captive and free-ranging conditions.

2. Methodology

2.1. Dataset

We first estimated age-specific survival for species in captivity from the database managed by the International Species Information System (ISIS). Since 1973, this network has collected individual animal data from 850 member institutions over the world (<http://www2.isis.org/>) and has kindly provided data for several comparative studies (e.g. Ricklefs and Scheuerlein, 2001; Ricklefs, 2010b; Müller et al., 2011; Young et al., 2011). For each individual, information such as sex, birth and death dates, and the country of birth and death are recorded. Since individuals of a given species are located in different institutions over the world, captive populations can be considered as 'meta-populations' consisting of many different subpopulations at each zoo. Thus, these 'meta-populations' describe the average performance of species in captivity and do not describe one specific population at a particular space and time, compared to data for free-ranging populations (see below). For this study, we followed the approach of Müller et al. (2010), using only complete cohorts of animals whose birth dates were known (thus excluding animals born in the wild), and none of which survived to the time of data collection (in other words, all individuals died within the observation interval). We collected information on age-specific survival in species living in free-ranging conditions (but not hunted) using the keywords 'life table' in the topic window of *Web of Knowledge*. We focused our search protocol on papers citing the two 'classic'

papers by Deevey (1947) and Caughley (1966). These two papers reported the first comprehensive analyses of age-specific survival and are therefore likely to be quoted by most relevant studies containing age-specific survival data for wild populations (Lemaître and Gaillard, 2013). Although information on age-specific survival is more limited for species in free-ranging populations than for species in captivity because it requires collecting long-term data in the field (Nussey et al., 2008), we ended up with a dataset of 22 species with estimates of age-specific survival for both sexes in both wild and captive conditions.

Methods used to assess age-specific survival differed markedly between studies, which can potentially influence inter-specific patterns of actuarial senescence (Péron et al., 2010). We thus included a quality factor for each free-ranging population ('0' for studies that used longitudinal data of marked individuals and '1' for cross-sectional studies of wild populations). Sample sizes were $n = 11$ for each category. The percentage of grass in the natural diet for each species was collected from the literature. This variable allows ranking species along a continuum from browsers to grazers (Müller et al., 2011). Finally, to test for an influence of male and female body mass on aging rates we gathered information on mammalian body masses from published reviews (e.g. Silva and Downing, 1995). All data are available online (see Appendix A1, Table A1).

2.2. Aging rates

A classical method to measure the rate of aging within a population is to fit mathematical functions to data describing age-specific survival or mortality (Ricklefs, 2008). In the present study, we measured aging rates by fitting i) generalized additive models (*GAM*) ($n = 22$ species) and ii) Gompertz models in species for which capture histories were available ($n = 7$ species).

To compute male and female aging rates for each species from our dataset in both environments (captive and wild), we used the *GAM* approach recently described in Jones et

al., (2008). The first step of this procedure was to determine the age at the onset of senescence. Following Jones et al., (2008), we defined the onset of senescence as the age at which survival is maximal or, in other words, the age at which survival starts to decrease. To estimate this peak of survival, we modelled survival as a function of age using generalized additive models (*GAM*) (Hastie and Tibshirani, 1990) following the *GAM* procedure from the *gam* package (Hastie, 2006). These *GAMs* are well suited to model traits such as survival since they do not make any assumption on the data distribution (Hastie and Tibshirani, 1990). Once the age at the peak of survival had been estimated, we measured the rate of aging as the slope of the linear regression of age-specific survival (i.e. *y* axis) against the unit of time (year, i.e. *x* axis) from the age at the onset of senescence to the maximum age for the species recorded in the life-table. Because survival is decreasing with age in mammals (Nussey et al., 2013), aging rates corresponded to the opposite of the slope. Importantly, to avoid under-estimation of aging rate due to the presence of a couple of high quality individuals living particularly long lives, we considered the maximum age for a species attained when age-specific survival was equal to 1 for the first time (when the few surviving individuals of an advanced age all survived to the next age class). Estimates for four species (African buffalo, *Syncerus caffer*; Bighorn sheep, *Ovis canadensis*; Reindeer and Roe deer) were available for more than one free-ranging population and we thus computed aging rate as the median value across the different populations.

We also measured aging rates using Gompertz models, but only with species where age-specific survival computed from capture-mark-recapture (CMR) models were available ($n = 7$ species; Pronghorn, *Antilocapra americana*; Alpine ibex, *Capra ibex*; Roe deer; Mountain goat, *Oreamnos americanus*; feral Soay sheep, *Ovis aries*; Bighorn sheep and Greater kudu, *Tragelaphus strepsiceros*). We first built the capture histories of captive and wild populations by reporting whether a given individual was observed alive (coded as '1') or not observed (coded as '0') at a given age from birth (captive populations) or from marking at 1 year of age

(wild populations). We then entered these data in a CMR software (M-SURGE, Choquet et al., 2004) to obtain maximum likelihood estimates of annual survival and detection probabilities. Detection probabilities were equal to 1 in captive populations and we used the best structure of detection probabilities identified in previous works for wild populations (Gaillard et al., 2004). We first fitted a fully age-dependent model (with one survival parameter for each age). We then fitted the Gompertz model by constraining the between-age variation in survival from the age at the onset of senescence determined by the GAM procedure onwards to be linear on a log(-log) scale. We performed this CMR modelling on sex- and species-specific datasets. In each case, we compared the suitability of the Gompertz model using the full age-dependent model as a reference following Gaillard et al., (2004)'s recommendations. All following results were unchanged if we used age where survival was maximal with the CMR modelling.

2.3. Statistical analysis

To test for differences in aging rates between captive and free-ranging populations of ruminants, we ran a series of mixed effect models including aging rate (log-transformed absolute value) as the dependent variable, environment ('captive' versus 'wild'), sex ('male' versus 'female'), data quality ('0' versus '1'), body mass (log-transformed), the percentage of grass in the natural diet and any relevant two-way interaction terms as fixed factors; and a variable 'species' as a random effect to control for pseudo-replication (sensu Hurlbert, 1984) issues. We selected the best models based on Akaike's information criterion (AIC) and AIC weights (w_i), which assess the relative likelihood of each model to be the best among all the fitted models (Burnham and Anderson, 2002). However, one important point in inter-specific studies is to control for non-independence between species due to shared ancestry (Harvey and Pagel, 1991), which was not done in these previous mixed effect models. Therefore, we completed our 'mixed effect models' approach by fitting 'phylogenetically controlled models'

to avoid any statistical bias due to phylogenetic inertia. We first constructed a phylogeny of all species included in our database using a published phylogenetic supertree of mammals with topology and branch lengths (Bininda-Emonds et al., 2007). Then we used phylogenetic generalized least-squares models (PGLS, procedure implemented in R by Gage and Freckleton, 2003) with a variance-covariance matrix extracted from the constructed phylogenetic tree, using the R-package APE (Paradis et al., 2004). This statistical method estimates an index of phylogenetic correlation ' λ ', which is further introduced into the analysis to control for the phylogenetic dependence (Freckleton et al., 2002). We ran models for males and females separately including differences in rate of aging between wild and captive populations as the dependent variables and data quality ('0' versus '1'), body mass (log-transformed), percentage of grass in the diet and any relevant two-way interaction terms as independent variables. Summary of PGLS models for both sexes separately are presented in the supplementary online materials. All analyses were conducted using R version 2.12.1 (R Development Core Team 2011). Unless otherwise stated, parameter estimates are given as \pm one standard error.

3. Results

3.1. Aging rate (GAM)

Aging rates measured by GAM methods were statistically different from 0 for all species in both environments (captive and wild) and for both sexes (Table A1). The best model explaining aging (Table A2) included the interaction between environment (captive and wild) and diet ($w_i = 0.81$; Table 1). Aging rate was stronger in populations living in free-ranging conditions (0.073 ± 0.060) than in populations living in captivity (0.021 ± 0.014). Thus, no captive population occurred in the first 25th highest aging rates of our dataset. The difference in aging rate between captive and wild populations increased with the increasing percentage of grass in the species diet (Fig. 1). We typically found the same results with

analyses corrected for phylogeny. Indeed, for both sexes tested separately the difference in aging rate between captive and wild populations was best explained by the percentage of grass in their diet (Table A3 and A4). Moreover, in these analyses λ was really low (< 0.1), which revealed a very weak impact of phylogeny and thus confirmed the accuracy of our results with the mixed-effects approach (Table A3 and A4). At this stage, it is worth noticing that the rate of aging for male Soay sheep in wild conditions was particularly high (rate = 0.37) compared to other aging rates (Table S1). We thus replicated the analyses after excluding male Soay sheep but results were qualitatively unchanged since the best model included multiplicative effects of environment and diet ($w_i = 0.77$; Table A5). Finally, we found no evidence that the difference in aging rate between wild and captive species differed between sexes, was influenced by the quality of the data for wild populations, or by the species body mass because all models including these factors performed poorly compared to the selected model (Table A2).

3.2. Aging rate (Gompertz)

Similarly to aging rate measured by *GAM*, Gompertz rates of aging were statistically different from 0 for all the seven species for which this method could be applied in both environments (captive and wild) and for both sexes (Table A1). As expected both aging rates were correlated (Spearman coefficient of correlation: $n = 14$; $r = 0.44$; $p = 0.02$). The best model included both environment (captive and wild) and body mass ($w_i = 0.93$; Table A6), which reveals that the rate of aging is higher in wild than in captive populations (0.28 ± 0.11 and 0.18 ± 0.12 in males for wild and captive populations respectively and 0.27 ± 0.01 and 0.15 ± 0.04 in females for wild and captive populations respectively) and that body mass tends to be marginally correlated with rate of aging (Table 2). Figures 2A and 2B display differences in aging rate from Gompertz model for males and females and show that in males only the mountain goat (*Oreamnos americanus*) has a stronger rate of aging in captive as

compared to wild populations. Contrary to the results on the rate of aging based on *GAM*, the effects of environment and diet did not have interacting effects on aging rate. This result is confirmed by supplementary analyses controlling for phylogeny in males and females where the best model explaining differences in aging rate between free-ranging and captive populations was in both cases the constant model ($w_i = 0.74$, $w_i = 0.83$; Table A7 and A8 respectively). Note, however, that in females (Fig. 2B), captive populations displayed higher aging rates than wild populations in roe deer, a typical browser species (Andersen et al. 1998).

4. Discussion

Using two different metrics to estimate the magnitude of aging (using *GAM* and Gompertz model), our study provides clear evidence that the strength of senescence can vary within species according to environmental conditions with stronger aging rates found in wild populations.

Elevated aging rates for free-ranging populations are particularly interesting in regard to recent advances in life-history theory. Life history strategies of vertebrate species are ranked along a slow-fast continuum (Gaillard et al., 1989; Stearns, 1992). Basically, species with a fast pace of life will have short lives, will allocate substantially to reproduction early in life and will suffer from a steep rate of aging (Stearns, 1992; Jones et al., 2008), which is the opposite to species with a slow pace of life such as ruminant species. However, there is now some evidence that life-history traits of a given species show a degree of flexibility in response to environmental factors (Reznick et al., 1990; Milot et al., 2011). For instance, the generation time - a reliable metric of a species ranking along the slow-fast continuum (Gaillard et al., 2005) and thereby a correlate of aging rate in vertebrates (Jones et al., 2008) - has been found to vary across populations in Pyrenean chamois (*Rupicapra pyrenaica*) (Crampe et al., 2006) and roe deer (Nilsen et al., 2009). Therefore, although the average rate

of aging for a species is determined by its position along the slow-fast gradient (Jones et al., 2008), some variation in aging rate can potentially occur in response to variation in environmental conditions during early life (Bronikowski and Promislow, 2005; Nussey et al., 2007) or due to human interference with reproductive output. Various predictions can arise from the close relationship between early life performance and rate of aging (Kirkwood, 1977). For example, species living in captivity with a low mortality during early life should senesce slowly, as compared to conspecifics under free-ranging conditions with a high mortality during early life, due for example to predation or environmental harshness (see Gaillard et al., 1998 for a review). This prediction is well supported by our results showing that wild ruminants living in zoos have consistently lower aging rates than their wild conspecifics. These findings differ from Ricklefs and Scheuerlein (2001) who did not report any difference in aging rate (based on Weibull parameters) between wild and captive mammalian populations. However, in their analysis, Ricklefs and Scheuerlein (2001) often compared species at the genus level (e.g. *Damaliscus lunatus* vs. *Damaliscus dorcas*, *Kobus kob* vs. *Kobus defassa*, *Ovis dalli* vs. *Ovis aries*) and such comparisons are complicated by between-species differences within a genus. For example, *O. dalli* and *O. aries* have different geographical distribution, and marked within-genus variation in body mass occurs (100-140 kg for *D. lunatus* vs. 60-70 kg for *D. dorcas*; 60-70 kg for *K. kob* vs. 130-200 kg for *K. defassa*).

Among the factors influencing differences in aging rates between free-ranging and captive ruminant populations, the natural diet appears to play an important role. Indeed, although species in captivity have generally lower aging rates than their conspecifics living in wild conditions, the difference in these aging rates measured using *GAM* increased with the percentage of grass in the species' natural diet. From a conservation perspective, this indicates that animals in zoos perform the better compared to free-ranging conditions the more they are grazers (see also Müller et al., 2010, 2011). The diet influence on aging rates was not detected

when we focused on CMR data collected for 7 species. However, the range in the percentage of grass in the natural diet was much smaller in this subset (from 5 % to 69 %) than in the total dataset of 22 species (from 2% to 99%), which together with the inevitably reduced sample size makes a statistically significant effect of diet more difficult to obtain. However, in females, the direction of the difference in aging rates between captive and wild populations qualitatively supported an effect of diet (Figure 2). The effect of diet parallels Müller et al., (2010)'s findings that browser species have higher life expectancy in free-living populations than in captive ones. Overall, our study suggests that diet is a driving factor of senescence in captive populations (see also Müller et al., 2011) and emphasizes the difficulty of keeping browser species in captivity (independently of their body mass) compared to grazer species (Clauss and Dierenfeld, 2008).

5. Conclusions

Our study provides two fundamental results in regards of current developments in ecology of aging. First, the rate of aging is not fixed for a given species but varies in response to variation in environmental conditions (see also Nussey et al., 2007 for a case study on red deer). Understanding more precisely what ecological factors slow or speed up the rate of aging and assessing the magnitude of this variation now constitute a promising avenue in the study of aging. Second, the relative success of a species in captivity can therefore be assessed through the use of rate of aging and is strongly dependent of the species' natural diet, at least in ruminants. Therefore, it would be particularly interesting to extend this comparative approach to other species whose diets in the wild and in captivity differ distinctively, such as omnivorous carnivores and primates (Clauss et al., 2006; Schwitzer et al., 2009). In the current context where zoos are expected to play a growing role in the protection of biodiversity (Conde et al., 2011), our study provides an innovative approach to detect species

having low survival performance in captivity and thus to improve the efficiency of conservation programs.

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Table 1: Parameter estimates from the best model explaining variation in aging rates (*GAM*). The effects of species, environment, diet, and the interaction between environment and diet are included in the selected model (see the method section for a full description of these variables). This model includes aging rates for both sexes of the 22 ruminant species present in our dataset.

		Variance	SD		
Random effects	Species	0.000	0.000		
	Residuals	0.595	0.771		
		Estimate	SE	<i>p</i>	
Fixed effects	Intercept	-3.230	0.238	< 0.001	
	Environment	0.401	0.336	0.118	
	Diet	0.007	0.004	0.030	
	Environment * Diet	0.018	0.005	0.001	

Table 2: Parameter estimates from the best model explaining variation in aging rates (Gompertz). The effects of species, environment and body mass are included in the selected model (see the method section for a full description of these variables). This model includes aging rate for both sexes of the 7 ruminant species for which survival estimates from capture mark recapture analyses were available.

		Variance	SD		
Random effects	Species	0.000	0.000		
	Residuals	0.239	0.489		
		Estimate	SE	<i>p</i>	
Fixed effects	Intercept	-3.614	1.438	< 0.01	
	Environment	-0.648	0.185	< 0.001	
	Body mass	0.212	0.131	0.06	

Figure Legends

Figure 1: Relationship between aging rates (log-transformed absolute value) measured by generalized additive models (*GAM*) and the percentage of grass in the diet of each species and for both sexes. Black points and solid regression line display the relationship for free-ranging populations while white points and dashed regression line display the relationship for captive populations.

Figure 2: Rate of aging estimated from Gompertz model for 7 conspecific pairs of mammals in wild and captive conditions. Rate of aging are displayed for males (A) and females (B). Solid lines represent species that have a higher rate of aging in captive populations than in wild populations. On the contrary black dashed lines represent species that have a higher rate of aging in wild populations than in captive populations.

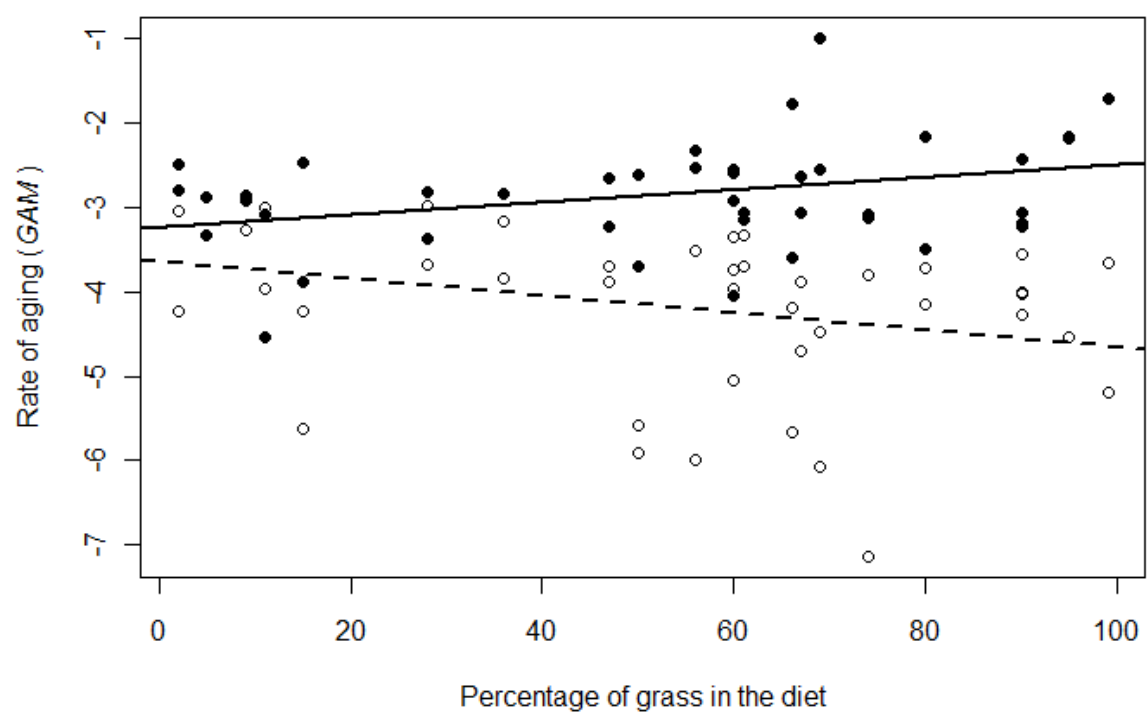


Figure 1

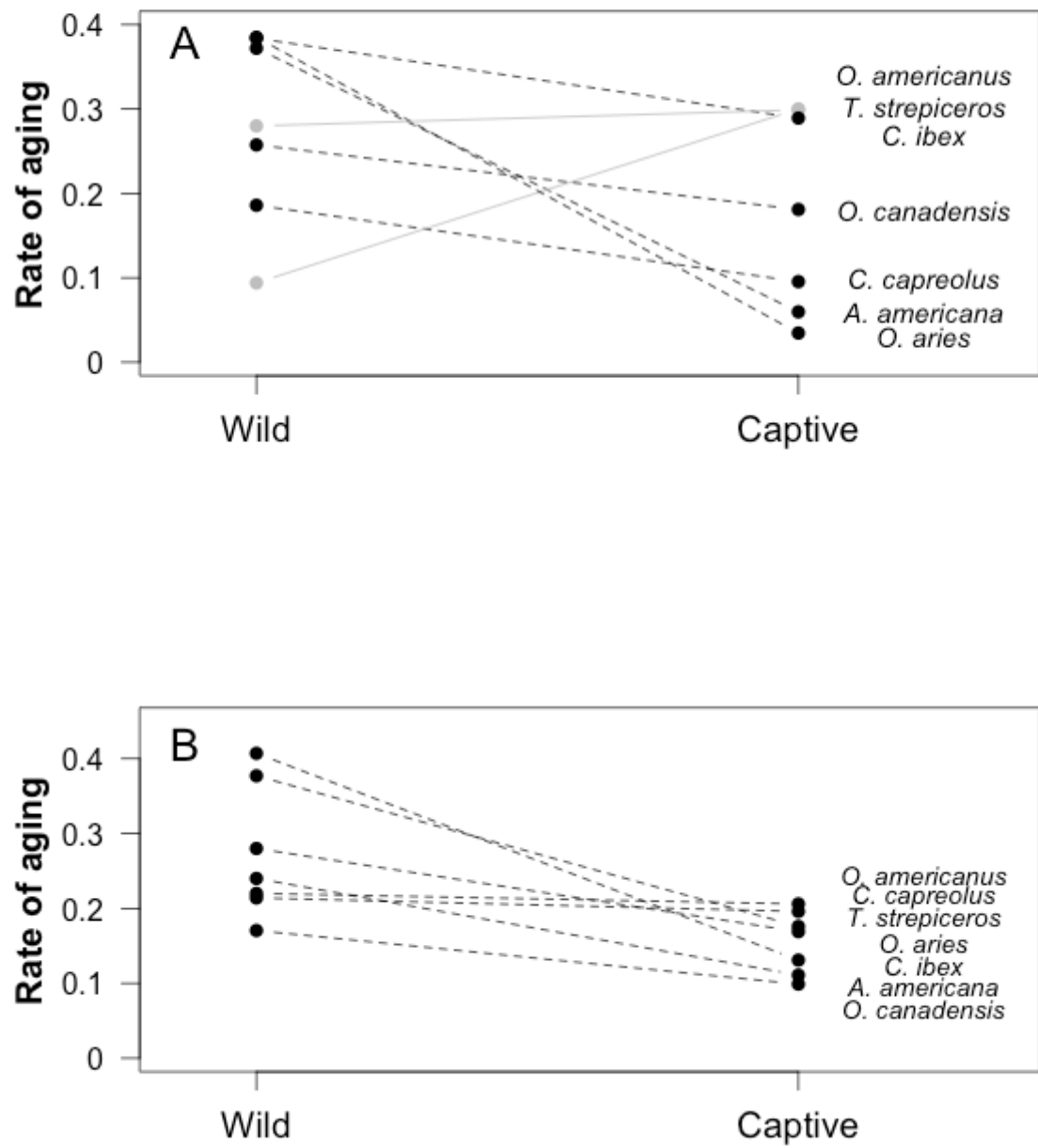


Figure 2